RESEARCH ARTICLE

Morphological specialisation for primary nectar robbing in a pollen specialist mining bee (Hymenoptera, Andrenidae)

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Abstract

The European mining bee species *Andrena lathyri* (Andrenidae) is a narrow specialist of flowers of *Lathyrus* and *Vicia* (Fabaceae), from which both females and males gain nectar by primary nectar robbing. Both sexes are equipped with a unique proboscis, which is much longer and more strongly angled than in most other *Andrena* bees including the most closely related species. The comparison between the shape of the proboscis and the interior of the host flowers combined with field observations revealed that the specialised mouthparts of *A. lathyri* precisely correspond to the dimensions of the flower interior and the position of the nectary, representing one of the few known examples of a morphological adaptation to primary nectar robbing in bees. For nectar uptake, the bee's head is inserted laterally under the standard petal before it is moved towards the flower base, thereby slitting the calyx longitudinally to a depth necessary to reach the nectary from inside the flower with the specialised proboscis. Nectar-robbing individuals of *A. lathyri* are able to adapt their behaviour to the different calyx lengths of their host flower species by slitting the calyx over varying distances. Except for the slit in the calyx, primary nectar robbing by *A. lathyri* does not damage any flower parts allowing for normal fruit development.

Introduction

Nectar that is deeply hidden inside a flower is usually only accessible to flower-visiting insects that possess long mouthparts. However, flower visitors with short mouthparts may also obtain deeply concealed nectar either by i) biting a hole into the plant tissue near the nectary through which the nectar is ingested ("primary nectar robbing"), ii) using an existing hole bitten by another flower visitor ("secondary nectar robbing"), iii) entering the flower through the normal entrance without touching the sexual flower organs for example due to small body size ("nectar thieving"), or iv) pushing the mouthparts between the petals of a polypetalous flower from the side or base, thereby gaining abbreviated access to the nectary ("base working") (Inouye 1980; Irwin et al. 2010). Compared to nectar-drinking insects that visit the flowers in a legitimate way, nectar robbers, nectar thieves and side workers usually do not pollinate the flowers during the process of nectar uptake.

Bees behaving as primary nectar robbers are usually not equipped with specialised morphological structures to get access to the nectar, but instead mostly use their unspecialised mandibles to bite through the plant tissue (Macior 1966; Inouye 1983). However, in the two bumblebee species *Bombus* (*Alpigenobombus*) *wurflenii* Radoszkowski and *B.* (*Bombus*) *occidentalis* Greene occurring in mountaineous areas of Europe and western North America, respectively, the apical edge of the female mandible is not regularly rounded as in most other bumblebees but equipped with several teeth, which are assumed to facilitate the perforation of the plant tissue (Inouye 1983; Reinig and Rasmont 1988; Rasmont et al. 2021). As both species are regular and frequent nectar robbers (Løken 1950; Maloof 2001; Goulson et al. 2013), the toothed mandibles likely represent a morphological specialisation for primary nectar robbing. The two species are only distantly related (Cameron et al. 2007), suggesting that this specialisation has independently evolved twice in the genus *Bombus*. In contrast to most other primary nectar robbers, carpenter bees of the genus *Xylocopa* do not use their mandibles to perforate the flower tissue, but instead slit the flowers with their maxillae (Schremmer 1972; Inouye 1983; Gerling et al. 1989). Interestingly, the maxillae appear to be highly adapted to nectar robbing since the galeae are heavily sclerotised, modified and tightly linked together forming a strong piercing organ, which is able to perforate even rather hard plant tissue (Schremmer 1972).

The European mining bee species *Andrena* (*Taeniandrena*) *lathyri* Alfken (Andrenidae) exclusively collects pollen on plants belonging to the Fabaceae (Westrich and Schmidt 1987). It is known to regularly act as a primary nectar robber on flowers of *Lathyrus* and *Vicia* (Westrich 1989; Teppner et al. 2016), a behaviour that may be obligatory in this species (Westrich 1989). *Andrena lathyri* differs from most other *Andrena* species including the closely related representatives of the subgenus *Taeniandrena* by a distinctly longer and strongly angled proboscis. This peculiar shape of the proboscis has to the best of our knowledge never been noticed by bee taxonomists nor has its function be explored by bee biologists. As both females and males of *A. lathyri* have identical mouthparts and regularly rob flowers, the peculiar proboscis is hypothesised here to be a morphological specialization for primary nectar robbing similar to the toothed mandibles of some *Bombus* species and the piercing maxillae of *Xylocopa*.

In the present study, we i) verify the narrow pollen host specialisation of *Andrena lathyri*, ii) confirm the species' habit as obligatory nectar robber, iii) analyse the morphology of the specialised proboscis by comparing it with that of closely related *A. (Taeniandrena)* species, iv) describe the bees' behaviour during nectar robbing and pollen collection, v) investigate the impact of primary nectar robbing on flower integrity and fruit formation, and vi) discuss the hypothesis that the peculiar proboscis of *A. lathyri* is a morphological adaptation to primary nectar robbing.

Methods

Bee species, flower species and study sites

Andrena lathyri is a 10–14 mm long ground-nesting solitary bee, which is distributed over large parts of Europe and Turkey (Gusenleitner and Schwarz 2022). In Central Europe, the species is widespread at lower elevations and regionally often abundant. It belongs to the subgenus *Taeniandrena*, which comprises about 35 Palearctic species with one species additionally introduced into the Nearctic (Gusenleitner and Schwarz 2002; Wood et al. 2021; Praz et al. 2022; Wood 2022; T. Wood, personal communication). All species of this subgenus, for which the pollen hosts are known, exhibit an exclusive or very strong preference for the pollen of Fabaceae (Westrich 1989; Praz et al. 2022). Together with *A. aberrans* Eversmann, which exclusively collects pollen on few genera of the tribe Genisteae, such as *Chamaecytisus* (Westrich 2018), *A. lathyri* is among the most strongly pollen-specialised representatives of *A. (Taeniandrena)* exploiting only two closely related genera of the tribe Fabeae, i.e., *Lathyrus* and *Vicia* (Westrich and Schmidt 1987; Schaefer et al. 2012). As the proboscis of *A. lathyri* is too short to reach the nectaries at the base of the *Lathyrus* and *Vicia* flowers, nectar cannot be ingested during legitimate flower visits. Instead, *A. lathyri* gains nectar by primary nectar robbing on its pollen hosts.

Lathyrus pratensis L. and *Vicia sepium* L. have typical legume flowers with a five-part calyx and corolla (Kugler 1970; Proctor et al. 2003; Fig. 6a–f). The calyx consists of five sepals, which are fused over most of their length ending in five apical lobes ("calyx teeth"). The corolla is composed of five petals, of which the uppermost petal is in dorsal position ("standard"), the median two petals are in lateral position ("wings") and the lowermost two petals are in ventral position largely concealed by the lateral wings. The lowermost two petals are ventrally and apically fused forming a boat-shaped structure ("keel") that encloses the single pistil and ten stamina, of which the dorsalmost stamen is free, whereas the filaments of the other nine stamina are fused to a staminal tube surrounding the pistil. The flowers have a secondary pollen presentation in that the pollen is shed at the late bud stage onto a dense brush of fine hairs near the apex of the style ("stylar brush"), from where it is removed by pollen-collecting bees. Nectar is produced at the base of the pistil in a nectary, which is longitudinally crossed by the filament of the uppermost stamen, either slightly above the nectary's upper rim in *L. pratensis* or slightly below the upper rim in *V. sepium* (Fig. 6e, f) The nectar is accessible only from above

the staminal tube, where there is a spacious empty flower interior due to the considerably arched base of calyx and standard. To drink nectar from the flowers of *L. pratensis*, flower visitors have to pass the proboscis through the rather narrow slit on either side of the stamen filament, while the nectar is slightly more easily accessible in *V. sepium* due to the lower position and the smaller width of the crossing stamen filament.

Field observations and experiments were performed in northern Switzerland near Rekingen (47°33'59"N, 8°18'41"E; site 1), Dagmersellen (47°13'28"N, 7°58'49"E; site 2) and Wädenswil (47°13'06"N, 8°40'45"E; site 3) from May to June 2021 and 2022.

Pollen host preferences

To verify the pollen host specialization of *Andrena lathyri* to flowers of *Lathyrus* and *Vicia*, we microscopically analysed the pollen contained in the hind leg scopa of 30 females collected at 30 different localities in Switzerland (n = 28) and Liechtenstein (n = 2) between 1914 and 2019 using the method described by Westrich and Schmidt (1986). Before removing pollen from the scopa, the amount of pollen was assigned to five classes, ranging from 5/5 (full load) to 1/5 (filled to one-fifth). The pollen grains were stripped from the scopa of one leg with a fine needle, embedded in glycerol gelatin on a slide and identified at a magnification of 400× to family, subfamily or genus level. While pollen of *Lathyrus* and *Vicia* can be easily distinguished from that of other Fabaceae taxa in Central Europe by light microscopy based on shape, ornamentation and size of the hydrated pollen grains, there are no reliable characters to separate *Lathyrus* from *Vicia* pollen in every case (Beug 2004). Therefore, pollen of these two closely related taxa was recorded as *Lathyrus*/*Vicia* type in the pollen samples examined.

Obligatory or facultative nectar robbing?

To clarify whether *Andrena lathyri* is an obligatory nectar robber on flowers of *Lathyrus* and *Vicia* or whether it exploits numerous other plant taxa for nectar, we analysed the flower-visiting data for *A. lathyri* contained in the database of the Wildbienen-Kataster Baden-Württemberg. At the time of data retrieval (August 2022), the database comprised 392 records of *A. lathyri*, which were distributed all over Baden-Württemberg, collected from 1988 to 2021 and provided by M. Haider, M. Klemm, V. Mauss, R. Prosi, A. Schanowski and H.-R. Schwenninger. For 189 out of these 392 records, the plant genus or plant species visited by *A. lathyri* was known.

Morphology of the proboscis

To analyse the morphology of the mouthparts of *Andrena lathyri*, the proboscis was examined under a stereomicroscope at a magnification of 40× and compared with that of nine other western Palearctic *Andrena* species of the subgenus *Taeniandrena*, i.e., *A. aberrans*, *A. afzeliella* (Kirby), *A. gelriae* Van der Vecht, *A. caesia* Warncke, *A. intermedia* Thomson, *A. leucopsis* Warncke, *A. poupillieri* Dours, *A. russula* Lepeletier, and *A. wilkella* (Kirby). For measurements, *A. wilkella* was selected as representative species for the

subgenus *Taeniandrena* as its proboscis was found to be morphologically identical to all *A.* (*Taeniandrena*) species other than *A. lathyri*. For five females and five males each of *A. lathyri* and *A. wilkella* originating from different localities in Switzerland, the length of the glossa from the lowermost point of the basiglossal sclerite to its apex and the intertegular width were measured with a micrometer scale to the nearest 0.025. For the same individuals, the angle between the dorsal surface of the labium's lateral sclerites and the anterior surface of the glossa was determined on close-up photographs taken with a Nikon D750 camera. The morphological terminology of the proboscis follows Michener (2000).

Nectar-robbing behaviour

To examine the behaviour of *Andrena lathyri* during primary nectar robbing, we observed females and males gaining nectar from flowers of *Lathyrus pratensis* and *Vicia sepium* with the aid of a threefold magnifying glass at site 1 on 16.6.2021 and at site 2 on 17.5.2022. In total, we observed about 90 nectar-robbing visits.

To understand the movements of the labium during nectar ingestion, two females of *Andrena lathyri* were observed in the laboratory drinking sugar water from a small bowl.

To investigate whether the long and angled proboscis of *Andrena lathyri* fits into the flower interior for nectar uptake, three consecutive sections of the labium of ten females and ten males originating from different localities in Switzerland were measured with a micrometer scale to the nearest 0.025 mm under a stereomicroscope at 40× magnification (Fig. 2a): i) length from the sclerotised base of the prementum to the sclerotised base of the labial palpi ("basal section"), ii) dorsal length of the intermediate section extending from above the sclerotised base of the labial palpi to and including the basiglossal sclerite ("intermediate section"), and iii) length of the anterior surface of the glossa from the dorsalmost point of the basiglossal sclerite to the tip of the glossa ("apical section"). The measured lengths were averaged over all 20 individuals, multiplied with ten and plotted onto a 10:1 drawing of an average-sized flower each of *Lathyrus pratensis* and *Vicia sepium* to optically evaluate the labium's fit to the flower interior and its ability to reach the nectary.

Pollen-collecting behaviour

To examine the behaviour of *Andrena lathyri* during pollen collection, we observed females harvesting pollen on flowers of *Vicia sepium* with the aid of a threefold magnifying glass at site 2 on 17.5.2022 and at site 3 on 24.5.2022. In total, we observed about 30 pollen-collecting visits.

Impact of nectar robbing on flower integrity and fruit development

To evaluate the damage caused to flowers by nectar-robbing individuals of *Andrena lathyri*, we collected 50 robbed flowers each of *Lathyrus pratensis* and *Vicia sepium* at site 1 on 4.5., 12.5. and 25.5.2022 and examined both corolla and calyx under a stereomicroscope at a magnification of 20–40×.

To investigate whether the fruits of flowers robbed by *Andrena lathyri* develop normally, 25 flowers of *Vicia sepium* that showed the typical sign of having been robbed, i.e., a longitudinal slit in the calyx (see below), were marked with coloured threads at site 3 on 24.5.2022. Two weeks later, the development of the fruits of the marked flowers was assessed.

Results

Pollen host preferences

All 30 female pollen loads of *Andrena lathyri* from Switzerland and Liechtenstein exclusively consisted of pollen of the *Lathyrus*/*Vicia* type (Fig. 1a). This finding supports the species' narrow pollen specialisation already postulated by Westrich and Schmidt (1987), who found 46 pollen loads from Germany, Austria, Poland and Greece to be composed only of *Lathyrus* and/or *Vicia* pollen.

Obligatory or facultative nectar robbing?

Based on the Wildbienen-Kataster dataset, 69 (87.3%) of 79 flower visits by females of *Andrena lathyri* and 102 (92.7%) of 110 flower visits by males were recorded on flowers of *Lathyrus*, such as *L. niger* (L.) Bernhardi, *L. pratensis* L. and *L. vernus* (L.) Bernhardi, and of *Vicia*, such as *V. angustifolia* L., *V. cracca* L., *V. sativa* L., *V. sepium* L. and *V. villosa* Roth (Fig. 1b). Considering that the females mostly collect both pollen and nectar during the same flower visit (see below) and the males exploit the flowers only for nectar, these figures suggest that *A. lathyri* only exceptionally gains nectar from flowers other than *Lathyrus* and *Vicia*, rendering the species an almost obligatory nectar robber.

Morphology of the proboscis

The comparison of the proboscis of *Andrena lathyri* with that of nine other *Andrena* species of the subgenus *Taeniandrena* revealed that the morphological differences between *A. lathyri* and its relatives are restricted to the labium, whereas the construction of the maxillae is identical.

The labium of *Andrena* (*Taeniandrena*) species consists of five main sclerotised parts (Fig. 2a, b): i) the prementum, which extends till the base of the labial palpi, ii) the two four-segmented labial palpi, which attach laterally to the end of the prementum, iii) a pair of lateral sclerites, which cover the base of the paraglossae from above and form together with the adjacent basiglossal sclerite an intermediate section between the end of the prementum and the anterior surface of the glossa, iv) the two paraglossae, which attach distal to the ventral end of the prementum, run along the lower margin of the two lateral sclerites and are distally bent outwards, and v) the glossa, which originates between the base of the paraglossae, tapers towards its apex and is densely beset with annulate hairs below the basiglossal sclerite.
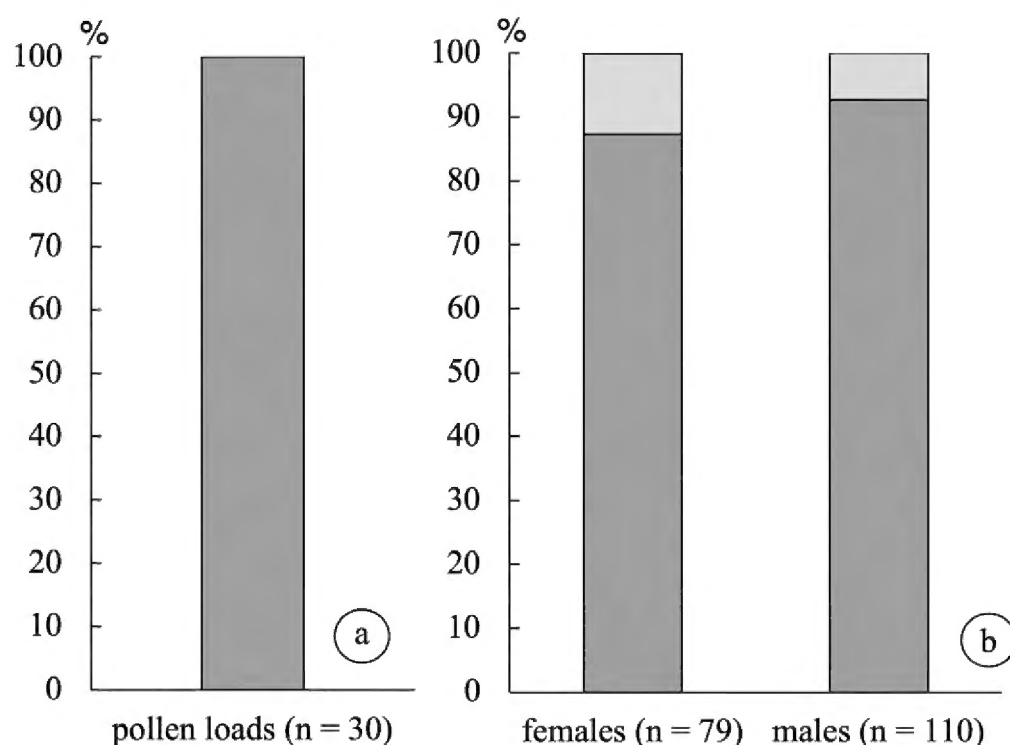
Figure 1. Pollen and nectar sources of *Andrena lathyri* **a** composition of female pollen loads **b** flower visits. Dark grey = *Lathyrus* and *Vicia* species, light grey = other plant species.

The labium of *Andrena lathyri* differs in two main respects from that of all other *A.* (*Taeniandrena*) species represented here by *A. wilkella* (Fig. 2). First, the glossa is on average 1.57 mm long in *A. lathyri* (range = 1.48–1.68 mm, n = 5 females and 5 males), whereas it is on average 0.50 mm long in *A. wilkella* (range = 0.45–0.55 mm, n = 5 females and 5 males). By correcting for the difference in body size, which is 10% smaller in *A. wilkella* based on intertegular width, the glossa of *A. lathyri* is about 2.9× longer than that of *A. wilkella*. Second, the angle between the dorsal surface of the lateral sclerites and the anterior surface of the glossa is on average 100.8° in *A. lathyri* (range = 91–109°, n = 5 females and 5 males), whereas it is on average 140.9° in *A. wilkella* (range = 130–152°, n = 5 females and 5 males). These differences result in a much longer and distinctly more strongly angled labium in *A. lathyri* compared to most other *Andrena* species including the closely related representatives of the subgenus *Taeniandrena*.
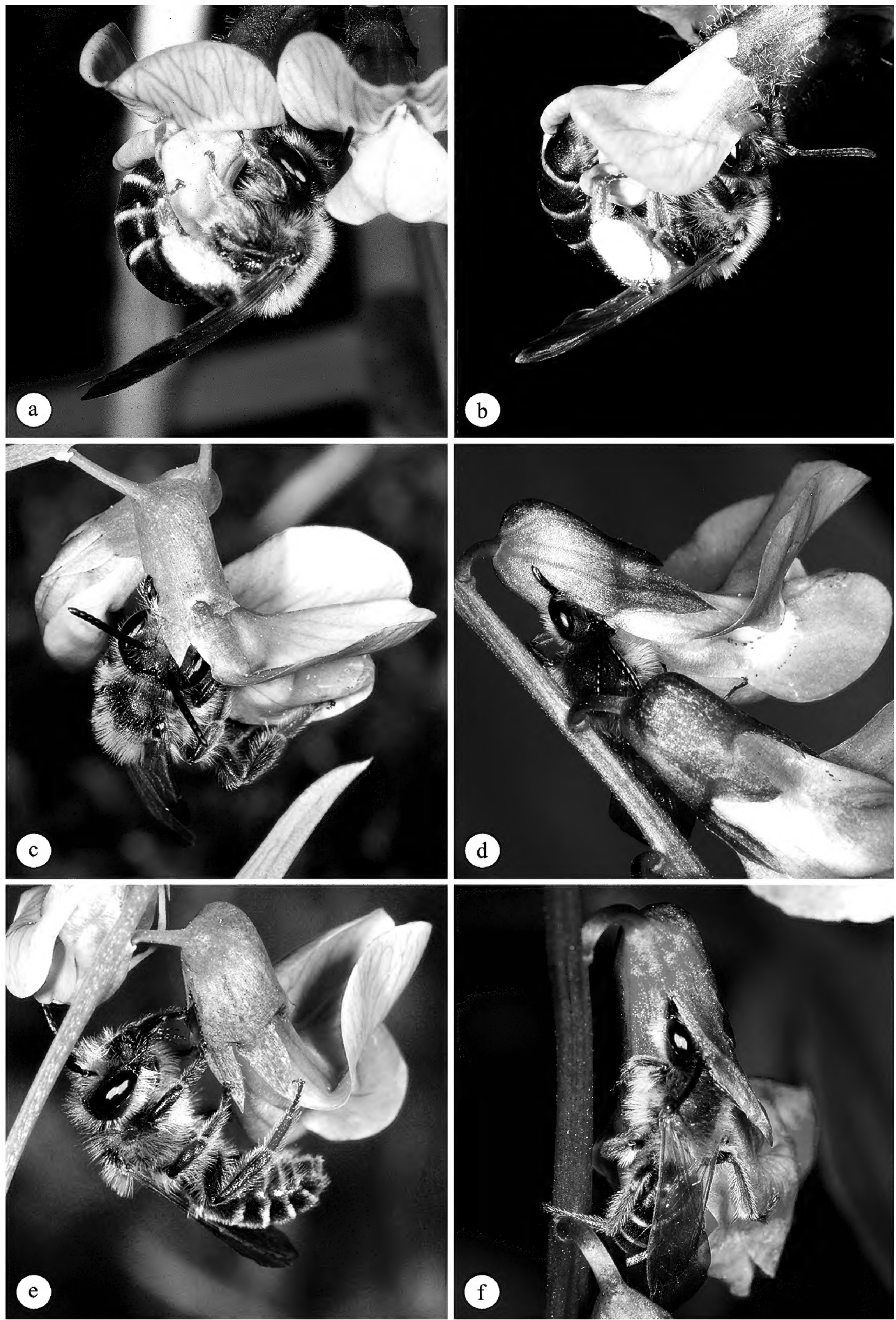
Nectar-robbing behaviour

The behaviour of nectar-robbing individuals of *Andrena lathyri*, which was very uniform, identical in both sexes and invariant between flowers of *Lathyrus pratensis* and *Vicia sepium*, can be divided into three phases. In the first phase, the bees crawled headfirst to the side of the flower and inserted the half-extended proboscis and the lower half of the head under the lower margin of the standard (Figs 3a, 6c, d). In the second phase, the bees moved the head between the inner side of the standard and the outer side of the wing towards the base of the flower (Fig. 3b); when the advancing head reached the calyx, the outer mandible was spread out (Fig. 3c), and by moving the head further towards the flower base, the calyx was torn open between the lowest and the second lowest calyx tooth (Fig. 3d); during advancing, the outer mandible was repeatedly moved up and down, which probably facilitated the process of tearing the rather hard calyx tissue by acting
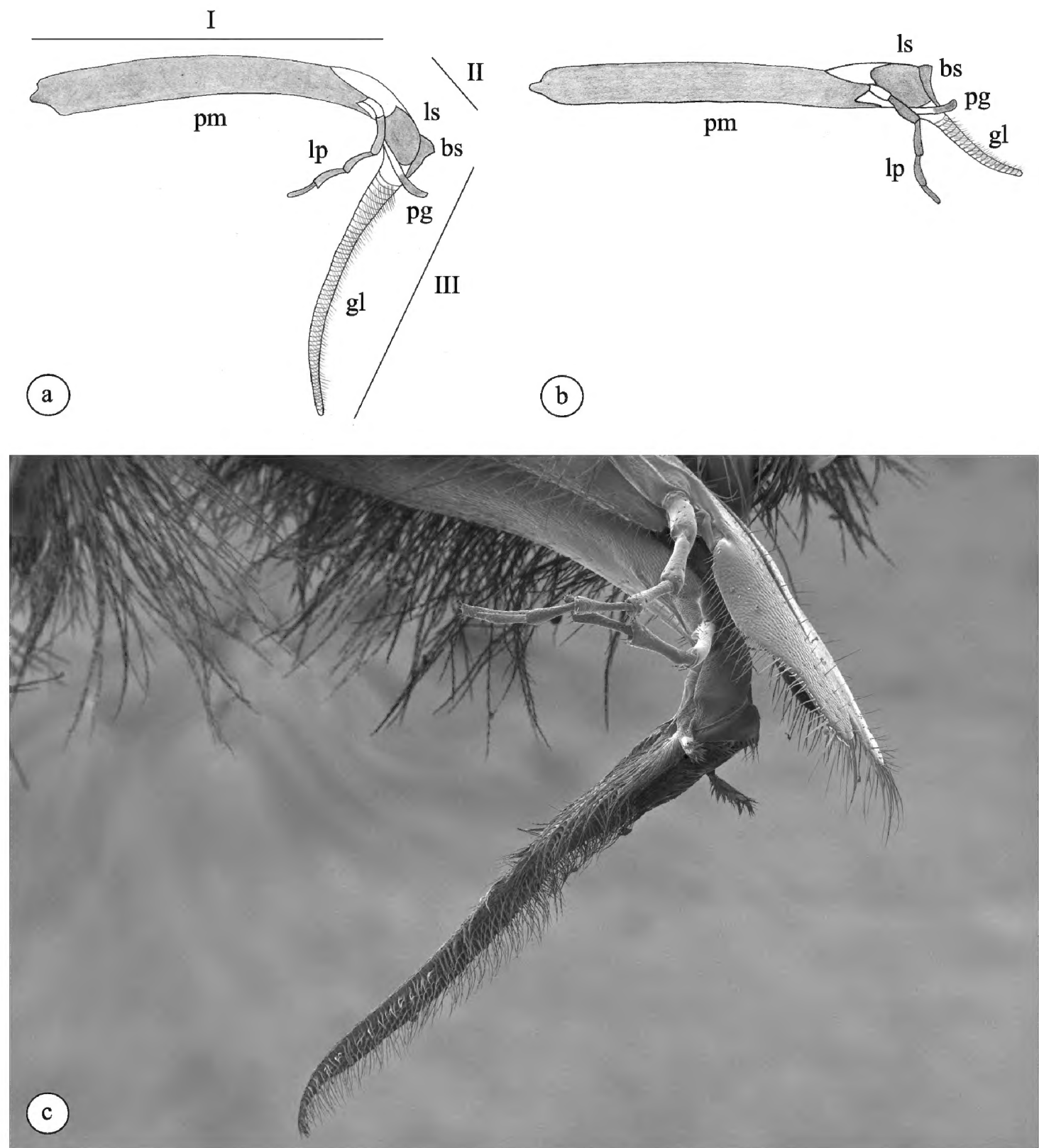
Figure 2. Mouthparts of *Andrena lathyri* and *Andrena wilkella* in lateral view **a** labium of *A. lathyri* **b** labium of *A. wilkella* **c** maxilla and labium of *A. lathyri*. pm = prementum, lp = labial palpus, ls = lateral sclerite, bs = basiglossal sclerite, pg = paraglossa, gl = glossa; I = basal section, II = intermediate section, III = apical section.

as an abutment or support, but not as cutting tool; instead, the calyx tissue tore due to the pressure of the advancing head; sometimes, a soft crackling sound was heard, which probably occurred when the tissue tore; at the end of this phase, the outer mandible rested on the calyx and the inner mandible, the proboscis and one compound eye were completely hidden inside the flower (Fig. 3d). In the third phase, the bees — holding

Figure 3. Nectar-robbing behaviour of *Andrena lathyri*. See text for details.

their head obliquely upwards from its ventral position relative to the flower —extended the proboscis inside the flower in longitudinal direction to the head upwards, so that the uppermost point of the angled proboscis was close to the upper roof of the flower base and the lowermost point, i.e., the apex of the glossa, reached the nectary from above to drink nectar (Fig. 4); after nectar uptake, the bees withdrew the proboscis from the calyx slit and left the flower (Fig. 3e).

In all observed nectar-robbing visits (n = 90), only one side of the calyx was slit, suggesting that the proboscis can empty the nectary from one side despite the longitudinally crossing stamen filament and that calyces slit on both sides originate from two different visits by *Andrena lathyri*.

How often individuals of *Andrena lathyri* gained nectar by secondary nectar robbing, i.e., by using an already existing calyx slit, could not be quantified exactly, because the observer's view of the flower base became obscured as soon as the bee crawled to the side of the flower to rob nectar. However, secondary nectar robbing occasionally occurred (Fig. 3f).

The observation of nectar-drinking females of *Andrena lathyri* in the laboratory revealed that the glossa can be moved far forwards and backwards in longitudinal direction to the body due to a ventral joint adjacent to the distal end of the prementum. In addition, the haired part of the glossa itself is movable to all sides, allowing for its precise guidance within the flower. In repose, the glossa is folded back over the dorsal surface of the prementum, which is embedded between the stipites of the maxillae within the proboscidial fossa on the underside of the head. For nectar ingestion, the prementum is moved downwards and forwards followed by the folding out of the glossa. At maximum extension of the proboscis, the sclerotised base of the prementum is situated roughly underneath the labrum resulting in a long maximal reach of the proboscis. By moving the prementum forward at different distances and/or bending the joint at the end of the prementum at varying angles, the mouthparts have a considerable flexibility to adjust to the specific interior of the host flowers, which is expected to slightly differ among the different species of *Lathyrus* and *Vicia* that are exploited by *A. lathyri* (see above).

The basal, intermediate and apical section of the labium of *Andrena lathyri* measured on average 1.91 mm, 0.30 mm and 1.74 mm, respectively (n = 10 females and males each). The true-to-scale plotting of these three sections, i.e. the labium at its maximum extension, onto flower drawings of *Lathyrus pratensis* and *Vicia sepium* revealed - in combination with the observed position of the bee's head during primary nectar robbing and the fact that the nectaries can be accessed only from above (see above) - that the bee's mouthparts precisely correspond to the dimensions of the flower interior and the position of the nectary (Fig. 4a–c).

Pollen-collecting behaviour

To collect pollen on flowers of *Vicia sepium*, the females of *Andrena lathyri* pushed the standard upwards with the front of the head, which created the necessary space for the movements of the fore legs (see below), and simultaneously pressed the wings sideways
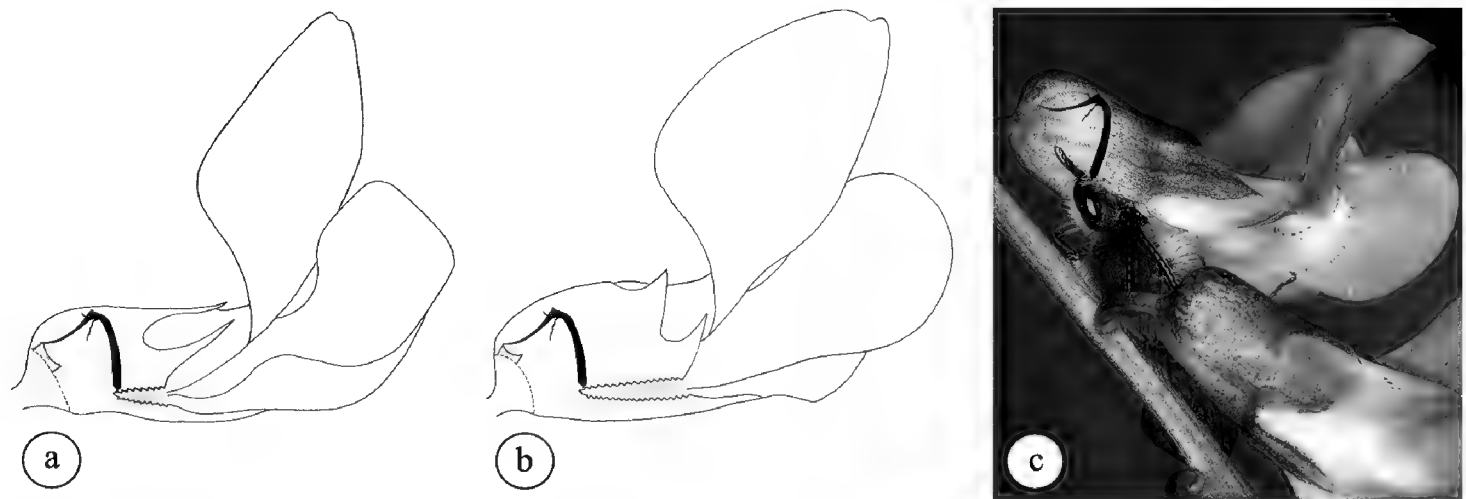
Figure 4. Maximally extended labium of *Andrena lathyri* plotted true to scale into the flower interior **a** *Lathyrus pratensis* **b, c** *Vicia sepium*. Black = labium, grey = nectary and calyx slit.

down with the middle and hind legs, which caused the keel to move downwards and the pollen-bearing stylar brush to emerge from the tip of the keel (Fig. 5a). The bees then harvested the pollen from the stylar brush by rapid strokes of the fore legs, which resulted in pollen masses adhering to both the pilosity of the foretarsi and the long hairs covering the underside of the maxillar stipites (Fig. 5b).

During most flower visits on *Lathyrus pratensis* and *Vicia sepium*, the females of *Andrena lathyri* first collected pollen, before crawling to one side of the flower to rob nectar. Occasionally, however, pollen-only and nectar-only visits also occurred.

Impact of nectar robbing on flower integrity and fruit development

Of the 50 corollae each of *Lathyrus pratensis* and *Vicia sepium* examined for damage by nectar-robbing individuals of *Andrena lathyri*, 81 (81%) were intact and 16 (16%) could not be properly assessed as the corolla was partly withered due to the late development stage of the flower; only three (3%) flowers of *V. sepium* were found to have a 1.8–5.8 mm long longitudinal crack near the lower margin of one of the two lateral wings, most probably caused by *A. lathyri* during nectar robbing.

Primary nectar robbing by *Andrena lathyri* on *Lathyrus pratensis* and *Vicia sepium* invariably resulted in a longitudinal slit in the calyx (Fig. 6a, b). This slit was located between the lowest and the second lowest calyx tooth in all 100 flowers examined with the exception of one flower of *V. sepium*, where the slit was located between the second lowest and the third lowest calyx tooth; interestingly, the corolla of the latter flower was one of the very few damaged by nectar robbing (see above), suggesting that this flower might possibly have been robbed by an unexperienced forager. The calyx was slit only on one side in 89 (89%) flowers examined, whereas it was slit on both sides in 11 (11%) flowers, probably resulting from two different flower visits (see above). The length of the calyx slit was significantly shorter in *L. pratensis* (range = 0.7–2.1 mm, median = 1.3 mm, n = 54) than in *V. sepium* (range = 2.0–3.9 mm, median = 2.8 mm, n = 57) (Mann-Whitney-U-test, U = 2.5, p < 0.001). In contrast, the distance between the end of the slit and the base of the flower, where the nectary is located in both

Figure 5. Pollen-collecting behaviour of *Andrena lathyri*. See text for details.

species, did not significantly differ between *L. pratensis* (range = 1.4–2.6 mm, median 2.1 mm, n = 54) and *V. sepium* (range = 1.4–2.9 mm, median = 2.2, n = 57) (Mann-Whitney-U-test, *U* = 1325.5, *p* = 0.206).

In 21 (84%) of the 25 marked flowers of *Vicia sepium*, the fruits developed normally in spite of having been robbed by *Andrena lathyri* (Fig. 6g, h), in one flower (4%) the ovary was withered and three flowers (12%) dropped off the plant for unknown reasons, overall suggesting a negligible negative impact of primary nectar robbing on fruit development.

Discussion

The present study verifies the narrow pollen specialization of *Andrena lathyri* to flowers of *Lathyrus* and *Vicia* (Fabaceae) and confirms the species' habit as a largely obligatory nectar robber on its pollen hosts.

Compared to the great majority of *Andrena* bees including the most closely related species (see Danforth et al. 2019), the proboscis of *A. lathyri* is exceptionally long due to a considerable elongation of the glossa and strongly bent due to an almost right angle between the short intermediate section of the labium and the glossa. This specialised proboscis precisely fits into the flower interior of *Lathyrus* and *Vicia* and its long and angled shape enables the bees to reach the nectary from above, which is the only way to gain nectar given the ventral position of the bee's head during nectar uptake. Because of this exact match between bee proboscis and host-flower interior, the specialised mouthparts of *A. lathyri* are interpreted here as a morphological specialisation for primary nectar robbing, which is in line with the findings that the proboscis is not actively involved in pollen harvesting and that females and males, which both rob flowers, possess identical mouthparts.
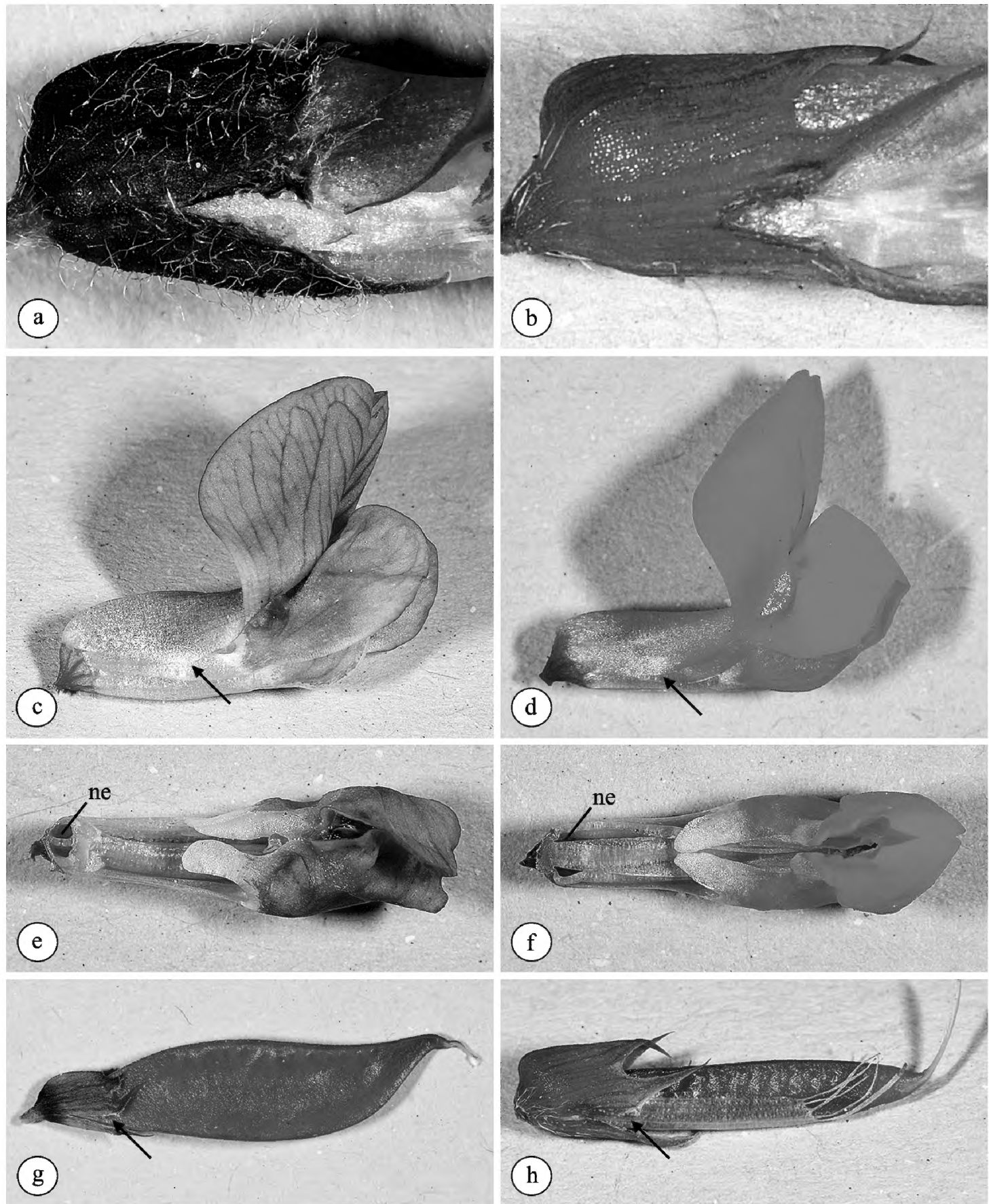
Figure 6. Flowers of *Vicia sepium* (left) and *Lathyrus pratensis* (right) **a, b** longitudinal slit in calyx due to primary nectar robbing by *Andrena lathyri* **c, d** flower with calyx removed showing lower side of standard (arrow), under which *A. lathyri* moves head and proboscis towards flower base **e, f** flower in top view with calyx, standard and wings removed showing nectary (ne), which is accessible only from above **g, h** normally developing fruits despite slit in the calyx (arrow) caused by *A. lathyri*.

Beside this morphological adaptation to primary nectar robbing, *Andrena lathyri* also exhibits behavioural specialisations, which include the insertion of proboscis and head under the lower margin of the standard of the *Lathyrus* and *Vicia* flowers and

the subsequent slitting of the calyx to a depth necessary to reach the nectary with the specialised proboscis. Interestingly, by slitting the calyx over a shorter distance in *L. pratensis* than in *V. sepium*, which has a longer calyx, nectar-robbing individuals of *A. lathyri* keep in both flower species the same distance between the end of the slit and the flower base, where the nectary is located. Slitting the calyx of *L. pratensis* over a similar length as in *V. sepium* would render nectar uptake by the specialised mouthparts impossible as in this case the proboscis would be too close to the flower base to reach the nectary from above. This finding reveals an amazing ability of nectar-robbing individuals of *A. lathyri* to adapt their behaviour to the different calyx lengths of their hosts.

The flowers of *Lathyrus* and *Vicia* species are characterised by a strongly arched base of calyx and standard leading to an almost right angle between the posterior side and the upper side of the flower base. This characteristic, which also occurs in other genera of the tribe Fabeae, such as *Pisum* or *Vavivolia*, results in a spacious flower interior above the nectary providing enough space for the movements of the specialised proboscis of *Andrena lathyri*. In contrast, the flower base of many other Fabaceae genera, such as *Genista*, *Hippocrepis*, *Lotus*, *Melilotus*, *Onobrychis* or *Trifolium*, is usually distinctly less strongly arched hardly leaving enough space for *A. lathyri* to gain nectar with its mouthparts. This difference in the shape of the flower base might contribute to the narrow flower specialisation of *A. lathyri* and probably renders host shifts to Fabaceae species other than those of the Fabeae difficult.

Primary nectar robbing by *Andrena lathyri* does not damage any flower parts except for a short slit on one side of the calyx, which is consistent with the findings that fruit development was not substantially impaired by nectar robbing and that at sites where *A. lathyri* was common many calyces at the base of well-developed fruits of both *Lathyrus pratensis* and *Vicia sepium* were slit. In contrast to the males of *A. lathyri*, which never come into contact with the sexual flower organs due to their illegitimate nectar visits, females are expected to pollinate the flowers during pollen collection, since both *Lathyrus* and *Vicia* have homogamous flowers with female and male reproductive organs maturing at the same time (Kugler 1970). Thus, primary nectar robbing by *A. lathyri* does not seem to have any significant negative effect on the reproduction of the bee's exclusive host plants, even more so as the flowers of *L. pratensis* and *V. sepium* are visited and pollinated by a multitude of different long-tongued bee species (Westrich 1989).

Conclusions

The peculiar proboscis of *Andrena lathyri* is one of the few known examples of a morphological adaptation to primary nectar robbing in bees and tightly binds the bee to its specific host plants, whose fruit development is not negatively affected by the illegitimate nectar gain.

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